THE INTRINSIC RATE OF NATURAL INCREASE
OF AN INSECT POPULATION

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1. INTRODUCTION

The intrinsic rate of increase is a basic parameter which an ecologist may wish to establish for an insect population. We define it as the rate of increase per head under specified physical conditions, in an unlimited environment where the effects of increasing density do not need to be considered. The growth of such a population is by definition exponential. Many authors, including Malthus and Darwin, have been concerned with this and related concepts, but there has been no general agreement in recent times on definitions. Chapman (1931) referred to it as 'biotic potential', and although he does state in one place that biotic potential should in some way combine fecundity rate, sex ratio and survival rate, he never precisely defined this expression. Stanley (1946) discussed a somewhat similar concept which he called the 'environmental index'. This gives a measure of the relative suitability of different environments, but it does not give the actual rate of increase of the insect under these different conditions. An index for the possible rate of increase under different physical conditions would at the same time provide a measure of the relative suitability of different environments. Birch (1945e) attempted to provide this in an index combining the total number of eggs laid, the survival rate of immature stages, the rate of development and the sex ratio. This was done when the author was unaware of the relevance of cognate studies in human demography. A sounder approach to insect populations based on demographic procedures is now suggested in this paper. The development of this branch of population mathematics is principally due to A. J. Lotka. From the point of view of the biologist, convenient summaries of his fundamental contributions to this subject will be found in Lotka (1925, Chapter 9; 1939 and 1945). A numerical example of the application of Lotka's methods in the case of a human population will be found in Dublin & Lotka (1925). The parameter which Lotka has developed for human populations, and which he has variously called the 'true' or 'inherent' or 'intrinsic' rate of natural increase, has obvious application to populations of animals besides the human species. The first determination of the intrinsic rate of increase of an animal other than man was made by Leslie & Ranson (1940). They calculated the 'true rate of natural increase' of the vole, Microtus agrestis, from age-specific rates of fecundity and mortality determined under laboratory conditions. With the use of matrices Leslie has extended these methods and, as an example, calculated the true rate of natural increase of the brown rat, Rattus norvegicus (Leslie, 1945). The author is much indebted to Mr Leslie for having drawn his attention to the possible application of actuarial procedures to insect populations. He has been completely dependent upon him for the methods of calculation used in this paper.

Before proceeding to discuss the reasons for the particular terminology adopted in this paper, it is necessary first to consider the true nature of the parameter with which we are concerned.

* This investigation was carried out at the Bureau of Animal Population, Oxford University, during the tenure of an overseas senior research scholarship from the Australian Science & Industry Endowment Fund.
2. BIOLOGICAL SIGNIFICANCE OF THE INTRINSIC RATE OF NATURAL INCREASE

The intrinsic rate of increase is best defined as the constant \( r \) in the differential equation for population increase in an unlimited environment,

\[
dN/dt = rN,
\]

or in the integrated form \( N_t = N_0 e^{rt} \),

where \( N_0 = \) number of animals at time zero,
\( N_t = \) number of animals at time \( t \),
\( r = \) infinitesimal rate of increase.

The exponent \( r \) is the difference between the birth-rate (\( b \)) and the death-rate (\( d \)) in the population \( (r = b - d) \). In some circumstances it may be more useful to know the finite rate of increase, i.e. the number of times the population multiplies in a unit of time. Thus, in a population which is increasing exponentially, if there are \( N_t \) individuals at time \( t \) then in one unit of time later the ratio

\[
\frac{N_{t+1}}{N_t} = e^r = \text{antilog}_e r = \lambda.
\]

Hence the finite rate of increase (\( \lambda \)) is the natural antilogarithm of the intrinsic (infinitesimal) rate of increase.

Any statement about the rate of increase of a population is incomplete without reference to the age distribution of that population, unless every female in it happens to be producing offspring at the same rate at all ages, and at the same time is exposed to a chance of dying which is the same at all ages. In such an inconceivable population the age of the individuals obviously has no significance. In practice, a population has a certain age schedule both of fecundity and of mortality. Now a population with constant age schedules of fecundity and mortality, which is multiplying in an unlimited environment, will gradually assume a fixed age distribution known as the stable age distribution (Lotka, 1925, p. 110). When this age distribution is established the population will increase at a rate \( dN/dt = rN \). Thus the parameter \( r \) refers to a population with a stable age distribution. The consideration of rates of increase in terms of the stable age distribution was one of the most important advances in vital statistics. In any other sort of population the rate of increase varies with time until a stable age distribution is assumed. There is, for example, no simple answer to the question: what is the rate of increase of \( x \) newly emerged adult insects in an unlimited environment? The rate will vary with time as immature stages are produced until the population has a stable age distribution. The rate of increase in the first generation might be given, but that is a figure of limited value. On the other hand, the maximum rate that it can ever maintain over an indefinite period of time is given by the rate of increase in a population of stable age distribution. That rate is therefore the true intrinsic capacity of the organism to increase. Thompson (1931) rejected the use of the exponential formula in the study of insect populations in preference for a method of dealing with the rate of increase as a ‘discontinuous phenomenon’. His paper should be consulted for the reasons why he considers a single index unsatisfactory in relation to the particular problems with which he was concerned.

If the ‘biotic potential’ of Chapman is to be given quantitative expression in a single index, the parameter \( r \) would seem to be the best measure to adopt, since it gives the intrinsic capacity of the animal to increase in an unlimited environment.* But neither ‘biotic potential’ nor ‘true rate of natural increase’ can be regarded as satisfactory descriptive titles. The word ‘potential’ has physical connotations which are not particularly appropriate when applied to organisms. There is a sense in which it might be better used with reference to the environment rather than the organism. Contrary to what it seems to imply, the ‘true rate of natural increase’ does not describe the actual rate of increase of a population at a particular point in time, unless the age distribution of that population happens to be stable. But it does define the intrinsic capacity of that population, with its given regime of fecundity and mortality, to increase. This point is clearly made by Dublin & Lotka (1925). More recently, Lotka (1945) has dropped the use of ‘true rate of natural increase’ for the more precise ‘intrinsic rate of natural increase’. It would seem desirable that students of populations should adopt the same terminology, irrespective of the animals concerned, and as ‘intrinsic rate of natural increase’ is more truly descriptive of the parameter \( r \) than other alternatives, its use is adopted in this paper.

The intrinsic rate of increase of a population may be calculated from the age-specific fecundity† and survival rates observed under defined environmental conditions. For poikilothermic animals these rates vary with physical factors of the environment such as temperature and humidity. Furthermore, within any

* For a discussion of the relative merits of this and other parameters in human demography reference should be made to Lotka (1945).

† Fecundity rate is used to denote the rate at which eggs are laid by a female. Some eggs laid are infertile and so do not hatch. The percentage ‘infertility’ is included in the mortality rate of the egg stage. It is usual amongst entomologists to denote the percentage of fertile eggs as the ‘fertility rate’. Demographers, on the other hand, use ‘fertility rate’ to denote the rate of live births. Since there is this other usage in entomology the term ‘fecundity rate’ is used throughout this paper as synonymous with the ‘fertility rate’ of the demographers.
given combination of physical factors, the fecundity and survival rates will vary with the density of the animals. Hence it is possible to calculate an array of values of $r$ at different densities. But particular significance attaches to the value of $r$ when the fecundity and survival rates are maximal, i.e. when density is optimal, for this gives the maximum possible rate of increase within the defined physical conditions. Between the whole array of physical conditions in which the animal can survive there is a zone where fecundity and survival rates are greatest and where, therefore, the intrinsic rate of increase will be greatest too. The zone within which the intrinsic rate of increase is a maximum may be referred to as the optimum zone. This is an arbitrary use of the word optimum and it does not imply that it is always to the advantage of the animal to increase at the maximum possible rate. The maximum intrinsic rate of increase under given physical conditions has importance from two points of view. It has a theoretical value, since it is the parameter which necessarily enters many equations in population mathematics (cf. Lotka, 1925; Volterra, 1931; Gause, 1934; Crombie, 1945). It also has practical significance. The range of temperature and moisture within which the insect can multiply is defined most precisely by that range within which the parameter exceeds zero. This will define the maximum possible range. In nature the range of physical conditions within which the species may be found to multiply may be less, since it is possible that effects of density and interspecific competition may reduce this range, and also the range of the optimum zone. These considerations are, however, beyond the scope of this paper; some discussion of them will be found in a review paper by Crombie (1947).

There are some important differences in the orientation with which the demographer and the student of insect populations face their problems. In human populations the parameter $r$ varies in different civilizations and at different times in one civilization, depending upon customs, sanitation and other factors which alter mortality and fecundity rates. The maximum possible value of $r$ does not enter into most demographic studies. In a population which is growing logistically the initial rate of increase is theoretically the maximum intrinsic rate of increase, and this latter value can be determined indirectly by calculating the appropriate logistic curve. Lotka (1927) has done this for a human population and so arrived at an estimate of a physiological maximum for man. This has theoretical interest only. In insect populations, on the other hand, the maximum value for the intrinsic rate of increase does assume considerable theoretical and practical significance, as has already been pointed out. The entomologist can readily determine the maximum values and this is his obvious starting-point. But the determination of $r$ at different stages in the population history of an insect, whether in an experimental population or in the field, offers many practical difficulties which have not yet been surmounted for any single species. The values which the entomologist has difficulty in determining are those which are most readily obtained for human populations. The crude birth-rates and crude death-rates of the population at specific stages in its history are precisely those indices with which the demographer works. His census data provides him with the actual age distribution which is something not known empirically for a single insect species. He can have a knowledge of age distribution even at intercensal periods, and under civilized conditions he can also determine the age-specific rates of fecundity and mortality which were in operation during any particular year. In insect populations this is at present impossible; one can only keep a number of individuals under specified conditions and determine their age-specific rates of fecundity and survival, and from these data $r$ can be calculated.

The fact that populations in nature may not realize the maximum value of their intrinsic rate of natural increase, does not negate the utility of this parameter either from a theoretical or a practical point of view. Having determined this parameter, the next logical step is to find out the extent to which this rate of increase is realized in nature. It is conceivable that some species, such as those which infest stored wheat or flour, may increase exponentially when liberated in vast quantities of these foodstuffs. This would imply that the insects could move out of the area in which they were multiplying with sufficient speed to escape density effects and that they had no gregarious tendencies. An exponential rate of increase may also occur in temperate climates in some plant-feeding species which only multiply in a short period of the year in the spring. In seasons with abundant plant growth the insect population may be far from approaching any limitation in the resources of the environment before the onset of summer retards the rate of increase. The population counts of *Thrips imaginis* in some favourable seasons in South Australia suggest such a picture (Davidson & Andrewartha, 1948).

### 3. Calculation of the Intrinsic Rate of Natural Increase

**a) Experimental data required**

The calculation of $r$ is based on the female population; the primary data required being as follows:

1. The female life table giving the probability of birth of being alive at age $x$. This is usually designated $L_x$ ($L_0 = 1$).

2. The age-specific fecundity table giving the
The intrinsic rate of natural increase of an insect population

mean number of female offspring produced in a unit of time by a female aged x. This is designated \( m_x \).

In the calculation of the stable age distribution the age-specific survival rates \( (l_x) \) of both the immature stages and the reproductive stages are required. For the calculation of \( r \) the life table of the adult and only the total survival of the immature stages (irrespective of age) are needed. In practice, the age-specific fecundity rates \( m_x \) will be established for some convenient interval of age, such as a week. If \( N \) eggs are laid per female alive between the ages \( x \) to \( x + 1 \) in the unit of time chosen, then \( m_x \) simply equals \( N/N \) when sex ratio is unity. It is assumed that this value occurs at the mid-point of the age group.

A numerical example is worked out for the rice weevil Calandra (Sitophilus) oryzae (L.) living under optimum conditions (29°C in weight of 14% moisture content). Data for the rates of development and survival of the immature stages, and the age-specific fecundity rates were obtained from Birch (1945a, b). The life table of adult females has not been determined experimentally, only the mean length of adult life being known. However, an estimate was obtained for purposes of these calculations by adapting the known life table of Tribolium confusum Duval (Pearl, Park & Miner, 1941) to Calandra oryzae, making the necessary reduction in the time scale. Since the mean length of life of Tribolium confusum in this life table was 198 days and the mean length of life of Calandra oryzae at 29°C was 84 days, one 'Calandra day' has been taken as equivalent to 2.35 'Tribolium days'. To this extent the example worked out is artificial, but, for reasons which will become evident later in the paper, it is unlikely that the error so introduced in the estimate of \( r \) is of much significance.

Before proceeding to outline direct methods of estimating \( r \) two other parameters must first be mentioned: the net reproduction rate and the mean length of a generation.

(b) The net reproduction rate

This is the rate of multiplication in one generation (Lotka, 1945) and is best expressed as the ratio of total female births in two successive generations. This we shall call \( R_0 \) and so follow the symbolism of the demographers. \( R_0 \) is determined from age-specific fecundity and survival rates and is defined as

\[ R_0 = \int_0^\infty l_x m_x dx, \]

where \( l_x \) and \( m_x \) are as already defined.

The method of calculating \( R_0 \) is set out in Table 1. The values of \( l_x \) are taken at the midpoint of each age group and age is given from the time the egg is laid. Since the survival rate of the immature stages was 0.90 the life table of adults reckoned from 'birth', i.e. oviposition, was the product: \( l_x \) for adults \( \times 0.90 \).

Development from the egg to emergence of the adult from the grain lasts 28 days and 4.5 weeks is the midpoint of the first week of egg laying. The product \( l_x m_x \) is obtained for each age group and the sum of these products \( \sum l_x m_x \) is the value \( R_0 \). In this particular example \( R_0 = 113.6 \). Thus a population of Calandra oryzae at 29°C will multiply 113.6 times in each generation.

Table 1. Showing the life table (for oviposition span) age-specific fecundity rates and the method of calculating the net reproduction rate \( (R_0) \) for Calandra oryzae at 29°C in wheat of 14% moisture content. Sex ratio is equal

<table>
<thead>
<tr>
<th>Pivotal age in weeks</th>
<th>((x))</th>
<th>((l_x))</th>
<th>((m_x))</th>
<th>((l_x m_x))</th>
</tr>
</thead>
<tbody>
<tr>
<td>4.5</td>
<td>0.87</td>
<td>20.0</td>
<td>17.400</td>
<td></td>
</tr>
<tr>
<td>5.5</td>
<td>0.83</td>
<td>23.0</td>
<td>19.090</td>
<td></td>
</tr>
<tr>
<td>6.5</td>
<td>0.81</td>
<td>15.0</td>
<td>12.150</td>
<td></td>
</tr>
<tr>
<td>7.5</td>
<td>0.80</td>
<td>12.5</td>
<td>10.000</td>
<td></td>
</tr>
<tr>
<td>8.5</td>
<td>0.79</td>
<td>12.5</td>
<td>9.875</td>
<td></td>
</tr>
<tr>
<td>9.5</td>
<td>0.77</td>
<td>14.0</td>
<td>10.780</td>
<td></td>
</tr>
<tr>
<td>10.5</td>
<td>0.74</td>
<td>14.5</td>
<td>9.250</td>
<td></td>
</tr>
<tr>
<td>11.5</td>
<td>0.66</td>
<td>14.5</td>
<td>9.370</td>
<td></td>
</tr>
<tr>
<td>12.5</td>
<td>0.59</td>
<td>11.0</td>
<td>6.490</td>
<td></td>
</tr>
<tr>
<td>13.5</td>
<td>0.52</td>
<td>9.5</td>
<td>4.940</td>
<td></td>
</tr>
<tr>
<td>14.5</td>
<td>0.45</td>
<td>2.5</td>
<td>1.125</td>
<td></td>
</tr>
<tr>
<td>15.5</td>
<td>0.36</td>
<td>2.5</td>
<td>0.900</td>
<td></td>
</tr>
<tr>
<td>16.5</td>
<td>0.29</td>
<td>2.5</td>
<td>0.800</td>
<td></td>
</tr>
<tr>
<td>17.5</td>
<td>0.25</td>
<td>4.0</td>
<td>1.000</td>
<td></td>
</tr>
<tr>
<td>18.5</td>
<td>0.19</td>
<td>1.0</td>
<td>0.190</td>
<td></td>
</tr>
</tbody>
</table>

\[ R_0 = 113.60 \]

The comparison of two or more populations by means of their net reproduction rates may be quite misleading unless the mean lengths of the generations are the same. Two or more populations may have the same net reproduction rate but their intrinsic rates of increase may be quite different because of different lengths of their generations. Consider, for example, the effect of moving the \( l_x m_x \) column in Table 1 up or down by a unit of age, \( R_0 \) remains the same but it is obvious that the generation times are now very different. For these reasons the parameter \( R_0 \) has limited value and it must always be considered in relation to the length of the generation \((T)\).

(c) The mean length of a generation

The relation between numbers and time in a population growing exponentially is given by

\[ N_T = N_0 e^{rt}. \]

When \( T = \) the mean length of a generation, then from the definition of net reproduction rate \( N_T/N_0 = R_0 \), hence

\[ R_0 = e^{rt}, \]

and

\[ T = \frac{\log_e R_0}{r}. \]
It follows that an accurate estimate of the mean length of a generation cannot be obtained until the value of \( r \) is known. For many purposes, however, an approximate estimate of \( T \) which can be calculated independently of \( r \) may be of use. Thus, although oviposition by the female is extended over a period of time, it may be considered as concentrated for each generation at one point of time, successive generations being spaced \( T \) units apart (Dublin & Lotka, 1925). For approximate purposes therefore it may be defined as

\[
T = \frac{\sum l_x m_x}{\sum l_x m_x}.
\]

We may thus consider the figures for the product \( l_x m_x \) given in the last column of Table 1 as a frequency distribution of which the individual items are each concentrated at the mid-point of each age group. The mean of this distribution is the approximate value of \( T \). In this particular example

\[
T = \frac{0.4390}{113.56} = 0.3 \text{ weeks}.
\]

If this were an accurate estimate of \( T \) we could proceed to calculate the value of \( r \) since, from the above equation relating \( R_0 \), \( r \) and \( T \), we have

\[
r = \frac{\log R_0}{T} = \frac{\log 113.56}{8.30} = 0.57 \text{ per head per week}.
\]

It will become evident in what follows that this is an underestimate of \( r \) owing to the approximate estimate of \( T \). The procedure does, however, serve to illustrate the nature of the parameter, and in some cases where \( r \) is small it may be a sufficiently accurate means of calculation (cf. for example, Dublin & Lotka, 1925). We shall proceed in the next section to an accurate method for the calculation of \( r \).

(d) The calculation of ‘\( r \)’

A population with constant age schedules of fecundity and mortality will gradually approach a fixed form of age distribution known as the stable age distribution (p. 16). Once this is established the population increases at a rate \( dN/dt = rN \) and the value of \( r \) may be calculated from the equation

\[
\int_0^\infty e^{-rx} l_x m_x dx = 1.
\]

For the derivation of this formula reference must be made to Lotka (1925) and the bibliography therein. The usual methods of calculation may be found in Dublin & Lotka (1925, Appendix) or Lotka (1939, p. 68 et seq.). For high values of \( r \), these methods may not be particularly satisfactory (Leslie & Ranson, 1940; Leslie, 1945, Appendix), and the computations, moreover, become very tedious. Some approximations to the rigorous procedures are justified in so far as the determination of the primary data which enter the above formula is of course subject to considerable error, arising from the normal variation in the organisms and conditions to which they are subjected in the experiments. It was considered that an estimate of \( r \), calculated to the second decimal place, was sufficient in these circumstances. The following approximate method was therefore adopted. It has the merit of being both simple and fast.

As an approximation we may write

\[
\sum e^{-rx} l_x m_x = 1.
\]

Here \( x \) is taken to be the mid-point of each age group and the summation is carried out over all age groups for which \( m_x > 0 \). A number of trial values are now substituted in this equation, in each case calculating a series of values \( e^{-rx} \) and multiplying them by the appropriate \( l_x m_x \) values for each age group. By graphing these trial values of \( r \) against the corresponding summation values of the left-hand side of the above expression, we may find the value of \( r \) which will make

\[
\Sigma e^{-rx} l_x m_x = 1.
\]

The whole procedure is greatly simplified by the use of 4-figure tables for powers of \( e \) (e.g. Milne-Thomson & Comrie 1944, Table 9). Since these tables only give the values of \( e^{\pm x} \) at intervals of \( 0.01 \) in the argument \( x \) up to \( e^{\pm 6} \), it may be convenient to multiply both sides of the equation by a factor \( e^k \) in order to work with powers of \( e \) which lie in the more detailed parts of the table. Thus, in the present example, \( k \) was taken as 7:

\[
e^{7r} \sum e^{-rx} l_x m_x = e^{7r} \sum e^{-rx} l_x m_x = 1097.
\]

A value of \( r \) was now sought which would make the left-hand side of this expression equal to 1097. The actual process of carrying out this simple computation is exemplified in Table 2. The summation of the expression is not carried beyond the age group centred at 13.5 because of the negligible contribution of the older age groups. It has already been mentioned that \( r \) is an infinitesimal rate of increase not to be confused with a finite rate of increase \( \lambda \) which equals antilog \( r \). In this particular example \( r = 0.076 \) and \( \lambda \) therefore has a value 2.14. In other words the population will multiply 2.14 times per week.

By reference to Table 2 it is clear that the relative weights with which the different age groups contribute to the value of \( r \) are given by the values \( l_x m_x e^{-rx} \) at each age group. It is of particular interest to observe the relation between values at successive age intervals (Table 3). The value of \( r \) is 56% accounted for by the first week of adult life. The first 2 weeks combined contribute 85% towards the final value and the first 3 weeks combined total 94%. The 13.5th week, on the other hand, contributes 0.02%. It
should not be inferred that adults 13.5 weeks old are of no importance since their eggs will eventually give rise to adults in the productive age categories. The biological significance of Table 3 is that the intrinsic rate of increase is determined to a much greater extent by the rate of oviposition in the first couple of weeks of adult life than by the total number of eggs laid in the life span of the adult, even although only 27% of the total number of eggs are laid in the first 2 weeks. With 

Table 2. Showing the method of calculating $r$ for Calandra oryzae at 29° by trial and error substitutions in the expression $\sum xe^{-rx}l_xm_x = 1097$

<table>
<thead>
<tr>
<th>Pivotal age group (x)</th>
<th>$l_xm_x$</th>
<th>$xe^{-rx}$</th>
<th>$xe^{-rx}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>4.5</td>
<td>17,400</td>
<td>3.58</td>
<td>3.53</td>
</tr>
<tr>
<td>5.5</td>
<td>19,090</td>
<td>2.82</td>
<td>2.76</td>
</tr>
<tr>
<td>6.5</td>
<td>12,510</td>
<td>2.06</td>
<td>1.90</td>
</tr>
<tr>
<td>7.5</td>
<td>10,000</td>
<td>1.30</td>
<td>1.22</td>
</tr>
<tr>
<td>8.5</td>
<td>9,875</td>
<td>0.54</td>
<td>0.45</td>
</tr>
<tr>
<td>9.5</td>
<td>10,780</td>
<td>-0.22</td>
<td>-0.32</td>
</tr>
<tr>
<td>10.5</td>
<td>9,250</td>
<td>-0.98</td>
<td>-1.09</td>
</tr>
<tr>
<td>11.5</td>
<td>9,570</td>
<td>-1.74</td>
<td>-1.86</td>
</tr>
<tr>
<td>12.5</td>
<td>6,490</td>
<td>-2.50</td>
<td>-2.62</td>
</tr>
<tr>
<td>13.5</td>
<td>4,940</td>
<td>-3.26</td>
<td>-3.39</td>
</tr>
<tr>
<td>[ \sum xe^{-rx}l_xm_x = 1108 ]</td>
<td>[ 1047 ]</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$r$ lies between 0.76 and 0.77 and by graphical interpretation $= 0.762$.

Table 3. The contribution of each age group to the value of $r$ when $r = 0.76$

<table>
<thead>
<tr>
<th>Pivotal age group (x)</th>
<th>$l_xm_xe^{-rx}$</th>
<th>Percentage contribution of each age group</th>
</tr>
</thead>
<tbody>
<tr>
<td>4.5</td>
<td>624.1</td>
<td>56.33</td>
</tr>
<tr>
<td>5.5</td>
<td>320.3</td>
<td>28.91</td>
</tr>
<tr>
<td>6.5</td>
<td>95.3</td>
<td>8.60</td>
</tr>
<tr>
<td>7.5</td>
<td>36.7</td>
<td>3.31</td>
</tr>
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<td>8.5</td>
<td>17.0</td>
<td>1.53</td>
</tr>
<tr>
<td>9.5</td>
<td>8.7</td>
<td>0.78</td>
</tr>
<tr>
<td>10.5</td>
<td>3.5</td>
<td>0.32</td>
</tr>
<tr>
<td>11.5</td>
<td>1.7</td>
<td>0.15</td>
</tr>
<tr>
<td>12.5</td>
<td>0.5</td>
<td>0.05</td>
</tr>
<tr>
<td>13.5</td>
<td>0.2</td>
<td>0.02</td>
</tr>
<tr>
<td>[ \sum x = 1108.0 ]</td>
<td>[ 100.00 ]</td>
<td></td>
</tr>
</tbody>
</table>

each successive week, eggs laid make a lessened contribution to the value of $r$. In this particular case this can be expressed by stating that for each egg laid in the first week of adult life it would require 2:1 times as many in the second week to make the same contribution to the value of $r$, $(2.1)^2$ in the third week and $(2.1)^n-1$ in the $n$th week. The ratio 2:1 is the ratio between successive weighting values $e^{-rx}$ (per egg) in Table 2. The importance of the first few weeks is further intensified by the fact that egg laying is at a maximum then. From these considerations it follows that in determining oviposition rates experimentally, the rates in early adult life should be found with the greatest accuracy. Of corresponding importance is the accurate determination of the pivotal age for the first age category in which eggs are laid. In the example being cited an error of half a week causes an error of 8% in the estimate of $r$.

The calculations were repeated ignoring the adult life table. The value of $r$ was then 0.77. Since the imposition of an adult life table only makes a difference of 1% in the value of $r$ it is evident that the life table is of little importance in this example. This is due to the fact already noted that the major contribution to the value of $r$ is made by adults in early life, and during early adult life survival rate is at a maximum. The life table may assume quite a different importance in a species with a different type of age schedule of fecundity or when the value of $r$ is lower.

4. THE STABLE AGE DISTRIBUTION

With a knowledge of the intrinsic rate of increase and the life table it is possible to calculate the stable age distribution and the stable female birth-rate of the population. Thus if $c_x$ is the proportion of the stable population aged between $x$ and $x + dx$, and $b$ is the instantaneous birth-rate

$$c_x = be^{-rx}l_x,$$

and

$$1/b = \int_0^\infty e^{-rx}l_xdx.$$  

For the usual methods of computation reference should be made again to Dublin & Lotka (1925). Mr Leslie has, however, pointed out to me another method of calculation which saves much of the numerical integration involved in the more usual methods. At the same time it is sufficiently accurate for our present purpose. If at time $t$ we consider a stable population consisting of $N_t$ individuals, and if during the interval of time $t$ to $t + 1$ there are $B_t$ female births, we may define a birth-rate

$$\beta = B_t/N_t.$$  

Then if we define for the given life table ($l_x$) the series of values $L_x$ by the relationship

$$L_x = \int_x^{x+1} l_xdx,$$

the stationary or 'life table' age distribution of the actuary,* the proportion ($p_x$) of individuals aged between $x$ and $x + 1$ in the stable population is given by

$$p_x = \beta L_x e^{-r(x+1)} + \int_x^{x+1} e^{-r(x+1)}dx,$$

where $x = m$ to $m + 1$ is the last age group considered in the complete life table age distribution. It will be noticed that the life table ($l_x$ values) for the complete

* For a discussion of $L_x$ see Dublin & Lotka (1936).
age span of the species are required for the computation of \( p_x \) and \( \beta \). But where \( r \) is high it will be found that for the older age groups the terms \( L_x e^{-r(x+1)} \) are so small and contribute so little to the value of \( \beta \) that they can be neglected.

The calculations involved are quite simple and are illustrated in the following example for *Calandra oryzae* at 29° (Table 4). Actually, in the present example, instead of calculating the values of \( L_x \), the values of \( L_x \) were taken at the mid-points of each age group. This was considered sufficiently accurate in the present instance. It should also be pointed out that whereas only the total mortality of immature stages was required in the calculation of \( r \), the age specific mortality of the immature stages is needed for the calculation of the stable age distribution. In this example the total mortality of the immature stages was 10%—and 98% of this mortality occurred in the first week of larval life (Birch, 1945d). Hence the approximate value of \( L_x \) for the mid-point of the first week will be 0.95 and thereafter 0.90 for successive weeks of the larval and pupal period (column 3, Table 4). The stable age distribution is shown in the fifth column of Table 4. This column simply expresses the fourth column of figures as percentages. It is of particular interest to note the high proportion of immature stages (95.5%) in this theoretical population. This is associated with the high value of the intrinsic rate of natural increase. It emphasizes a point of practical importance in estimating the abundance of insects such as *C. oryzae* and other pests of stored products. The number of adults found in a sample of wheat may be quite a misleading representation of the true size of the whole insect population. Methods of sampling are required which will take account of the immature stages hidden inside the grains, such, for example, as the ‘carbon dioxide index’ developed by Howe & Oxley (1944). The nature of this stable age distribution has a bearing on another practical problem. It provides further evidence to that developed from a practical approach (Birch, 1946) as to how it is possible for *C. oryzae* to cause heating in vast bulks of wheat, when only a small density of adult insects is observed. It is not an unreasonable supposition that the initial rate of increase of insects in bulks of wheat may approach the maximum intrinsic rate of increase and therefore that the age distribution may approach the stable form. Nothing, however, is known about the actual age distribution in nature at this stage of an infestation.

### Table 4. Calculation of the stable age distribution of *Calandra oryzae* at 29° when \( r = 0.76 \)

<table>
<thead>
<tr>
<th>Age group ((x))</th>
<th>( L_x ) ( e^{-r(x+1)} )</th>
<th>( L_x e^{-r(x+1)} )</th>
<th>( 100 \times L_x e^{-r(x+1)} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( x )</td>
<td>( 0.05 )</td>
<td>0.4677</td>
<td>0.4431</td>
</tr>
<tr>
<td>1</td>
<td>0.90</td>
<td>0.2187</td>
<td>0.1968</td>
</tr>
<tr>
<td>2</td>
<td>0.90</td>
<td>0.1022</td>
<td>0.0902</td>
</tr>
<tr>
<td>3</td>
<td>0.90</td>
<td>0.0473</td>
<td>0.0434</td>
</tr>
<tr>
<td>4</td>
<td>0.87</td>
<td>0.0237</td>
<td>0.0219</td>
</tr>
<tr>
<td>5</td>
<td>0.83</td>
<td>0.0104</td>
<td>0.0086</td>
</tr>
<tr>
<td>6</td>
<td>0.81</td>
<td>0.0049</td>
<td>0.0039</td>
</tr>
<tr>
<td>7</td>
<td>0.80</td>
<td>0.0024</td>
<td>0.0019</td>
</tr>
<tr>
<td>8</td>
<td>0.79</td>
<td>0.0010</td>
<td>0.0009</td>
</tr>
<tr>
<td>9</td>
<td>0.77</td>
<td>0.0005</td>
<td>0.0004</td>
</tr>
<tr>
<td>10</td>
<td>0.74</td>
<td>0.0002</td>
<td>0.0002</td>
</tr>
<tr>
<td>11</td>
<td>0.66</td>
<td>0.0001</td>
<td>0.0001</td>
</tr>
<tr>
<td>12</td>
<td>0.59</td>
<td>0.0000</td>
<td>0.0000</td>
</tr>
<tr>
<td>13</td>
<td>0.52</td>
<td>0.0000</td>
<td>0.0000</td>
</tr>
<tr>
<td>14</td>
<td>0.45</td>
<td>0.0000</td>
<td>0.0000</td>
</tr>
</tbody>
</table>

\[
\beta = 0.8116704 \times 100 = 0.000024
\]

5. THE INSTANTANEOUS BIRTH-RATE AND DEATH-RATE

We have already defined a birth-rate \( \beta \) by the expression

\[
1/\beta = \sum_{x=0}^{m} L_x e^{-r(x+1)}.
\]

This is not, however, the same as the instantaneous birth-rate \( (b) \) where \( r = b - d \). In personal communications Mr Leslie has provided me with the following relationship between these two birth-rates.

\[
b = \frac{r\beta}{e^r - 1}.
\]

Thus, in the example for *C. oryzae*, we have 1/\( \beta = 0.8116704 \) (Table 4), \( r = 0.76 \) and thus \( b = 0.82 \) and the difference between \( r \) and \( b \) is the instantaneous death-rate \( (d) = 0.06. \)

The instantaneous birth-rate and death-rate are widely used by students of human populations. The insect ecologist is more likely to find greater use for the finite rate of increase \( \lambda \) (natural antilog).

6. THE EFFECT OF TEMPERATURE ON '\( r'\)

As an illustration of the way in which the value of \( r \) varies with temperature and the corresponding changes in rate of development, survival and fecundity, an estimate of \( r \) for *C. oryzae* has been made for two temperatures (23°C 33.5°C) on either side of the optimum (29°C). The span of adult life at 23°C is about the same as at the optimum 29°C and so the same life table has been applied. Even although the egg laying is more evenly distributed throughout adult life the life table makes little difference to the value of \( r \). Furthermore, the first 2 weeks of adult life carry a weight of 59% of the total weight of all age groups in the determination of the value of \( r \). For every egg laid in the first week of adult life it would require 1.5
The intrinsic rate of natural increase of an insect population

times as many eggs in the second week to make the same contribution to the value of \( r \), and 2.3 times as many eggs in the third week to have the same effect. The relative weight of each week decreases less with successive weeks at 23° than at 29°. This is associated with the lower oviposition rates and the longer duration of the immature stages at 23°.

At 33.5° egg laying cases after the fourth week of adult life, the mortality of adults during these 4 weeks is not high and so the estimate of \( r \) obtained without a life table may not be very different from the true value.

Table 5. Showing the values of \( l_x \), \( m_x \) and the estimate of \( r \) for Calandra oryzae at 23° and 33.5°

<table>
<thead>
<tr>
<th>Pivotal age in weeks</th>
<th>( l_x )</th>
<th>( m_x )</th>
<th>Pivotal age in weeks</th>
<th>( l_x )</th>
<th>( m_x )</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.5</td>
<td></td>
<td></td>
<td>0.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Immature 0.9</td>
<td></td>
<td></td>
<td>Immature 0.25</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6.5</td>
<td></td>
<td></td>
<td>8.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7.5</td>
<td>0.87</td>
<td>9.0</td>
<td>9.5</td>
<td>0.25</td>
<td>6.0</td>
</tr>
<tr>
<td>8.5</td>
<td>0.83</td>
<td>11.0</td>
<td>10.5</td>
<td>0.25</td>
<td>3.5</td>
</tr>
<tr>
<td>9.5</td>
<td>0.81</td>
<td>11.5</td>
<td>11.5</td>
<td>0.25</td>
<td>3.0</td>
</tr>
<tr>
<td>10.5</td>
<td>0.80</td>
<td>12.0</td>
<td>12.5</td>
<td>0.25</td>
<td>1.0</td>
</tr>
<tr>
<td>11.5</td>
<td>0.79</td>
<td>11.5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12.5</td>
<td>0.77</td>
<td>13.0</td>
<td>( r = 0.12 ) per head per week</td>
<td></td>
<td></td>
</tr>
<tr>
<td>13.5</td>
<td>0.74</td>
<td>11.5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>14.5</td>
<td>0.66</td>
<td>11.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15.5</td>
<td>0.60</td>
<td>10.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>16.5</td>
<td>0.52</td>
<td>11.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>17.5</td>
<td>0.45</td>
<td>12.5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>18.5</td>
<td>0.36</td>
<td>10.5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>19.5</td>
<td>0.29</td>
<td>11.5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>20.5</td>
<td>0.25</td>
<td>4.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>21.5</td>
<td>0.19</td>
<td>2.0</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

With adult life table \( r = 0.43 \) per head per week.
Without adult life table \( r = 0.44 \) " " "

7. DISCUSSION

In order for a species to survive in a particular environment it may need to have evolved a certain minimum value for its intrinsic rate of natural increase. If its rate of increase is less than this it may succumb in the struggle for existence. It does not necessarily follow that the higher the intrinsic rate of increase the more successful will the species be. Evolution may operate to select species with an intrinsic rate of increase which is both large enough to enable them to compete successfully with other species and small enough to prevent a rate of multiplication which would exhaust the food supply in the environment. Whatever is the minimum necessary value of \( r \) it could be attained along more than one route, since \( r \) has a number of component variables; the length of development of the immature stages, the survival rate of the immature stages, the adult life table and the age-specific fecundity schedule. These components enter into the value of \( r \) with various weights, and it is suggested in the discussion which follows that a knowledge of their relative contributions may provide a clue to the significance of the life patterns characteristic of different species. There is clearly a pattern in the seasonal environment too, which must be considered at the same time. A hot dry period, for example, may necessitate a prolonged egg stage. In an environment which has relatively uniform physical conditions all the year round, these complicating factors are at a minimum, e.g. a tropical forest or the micro-environment of a stack of wheat.

(1) Consider first the length of the immature stages (non-reproductive period) in relation to the span of egg laying and the age schedule of fecundity. The earlier an egg is laid in the life of the insect the greater is the contribution of that particular egg to the value of \( r \). In illustration we may consider the age schedule of fecundity for C. oryzae at 29°. Since over 95% of the value of \( r \) is determined by the eggs laid in the first 4 weeks of adult life (Table 3) we can, for purposes of illustration, ignore the remaining period.

At 29° the immature stages of C. oryzae last 4 weeks and the maximum rate of egg laying is 46 eggs per week (Table 1). Now the same value of \( r \) (0.76) is given in a number of imaginary life cycles by reducing the length of the immature stages along with a reduction in the rate of egg laying and alternatively by increasing both the length of the immature stages and the number of eggs laid (ordinary figures, Table 6). In Table 6 the age schedule of fecundity is kept proportionate in each case. In the extreme examples if the immature stages could develop in a week, an oviposition maximum of 5 eggs per week would give the same rate of increase as the imaginary insect which took 6 weeks to develop and had an oviposition maximum of 204 eggs per week. The imaginary life cycles have been calculated from the ratio \( (2^1:1) \) for successive weighting values \( (e^{r-r}) \) in Table 2.

The question might now be asked, what determines the particular combination which the species happens to possess? In the specific example in question, if the larva took 6 weeks to develop the adult would need to lay 200 eggs per week. But it now becomes necessary to consider the behaviour pattern, for C. oryzae bores a hole in the grain of wheat for every egg which is laid. The whole process of boring and egg laying occupies about 1 hr. per egg. So that with this particular mode of behaviour 24 eggs per day would be an absolute maximum. There must of course also be some physiological limit to egg production. For a larger insect the physiological limit might be less restrictive provided that the size of the egg does not increase.
proportionately with the size of the insect. In considering this possibility, ecological considerations are important, for *C. oryzae* is adapted to complete its development within a grain of wheat and a size limit is set by the length of the grain. There is, in fact, a strain which is found in maize kernels in Australia and this is considerably larger than the so-called ‘small strain’ (Birch, 1944). Furthermore, the larger insect would probably require a longer time to complete development (which is actually the relationship observed between the small and large strains) and this would operate to reduce the value of *r*. In considering the possibilities in the opposite direction, there is obviously a limit below which the length of development could not be reduced any further. A species of smaller size could doubtless develop in a shorter time and on this merit might be a more successful mutation. But the question then arises whether a smaller species could command muscles and mandibles of sufficient strength to chew whole grain. Grain-feeding species of beetles which are smaller than *C. oryzae* are in fact scavengers rather than feeders on sound grain. Thus it would seem that a balance is struck somewhere between the minimum time necessary for development and the maximum possible rate of egg laying, and this is conditioned by the behaviour pattern of the insect and the particular ecology of its environment.

For a maximum value of *r* the optimum age schedule of fecundity is one which has an early maximum. In an imaginary schedule for *C. oryzae* a concentration of 71 eggs in the first week of egg laying would give the same value of *r* (0.76) as 141 eggs distributed over 4 weeks.

*Age schedule of fecundity of Calandra oryzae at 29°*

<table>
<thead>
<tr>
<th>Weeks</th>
<th>Actual</th>
<th>Imaginary</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>40</td>
<td>71</td>
</tr>
<tr>
<td>1</td>
<td>40</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>46</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td>30</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>25</td>
<td>71</td>
</tr>
</tbody>
</table>

The relative advantage of this type of fecundity schedule is less, the smaller the value of *r*. At 23° the value of *r* for *C. oryzae* is 0.43 and the eggs laid in the first week of adult life are worth (1.5)^n−1 eggs in the nth week (compare this with the value of (2.1)^n−1 when *r* = 0.76). The actual oviposition time curve at 23° has no distinct peak as at 29° (Tables 1 and 5).

There is a wide variation in the nature of the age schedule of fecundity amongst different species of insects with perhaps the tsetse fly and the lucerne flea illustrating contrasting extremes. Whereas tsetse flies (*Glossina*) deposit single larvae spaced at intervals of time, the ‘lucerne flea’ (*Smyththrus viridis*) deposits its eggs in one or two batches of as many as 120 at a time (Maclagan, 1932). The particular advantage of this mode of oviposition must be tremendous, and is probably responsible in part for the great abundance of this collemboan and possibly other members of the same order, which, as a whole, are among the most abundant insects in nature. This is of course speculative and much more information is required before any generalizations can be made. Another interesting category are the social insects, since only one female of the population (in termites and the hive-bee) or a few (in social wasps) are reproductive. A theoretical consideration of the relative merits of one queen and many queens might throw more light on the evolution of these systems, especially as they relate to differences in behaviour.

The relation between the length of the pre-reproductive stages and the nature of the age-fecundity schedule is in part dependent upon the nature of the seasonal changes in the environment. Life histories may be timed so that the reproductive and feeding stages coincide with the least hostile season of the year. Diapause, aestivation and hibernation are some of the adaptations which ensure this. They have particular significance too in determining the age distribution of the initial population in the reproductive

Table 6. *Showing the actual relation between the length of the immature stages and the age schedule of fecundity for Calandra oryzae at 29° (black figures) and some theoretical possibilities which would give the same intrinsic rate of increase (r = 0.76). The length of the immature stages is shown in the left of the table; figures in the body of the table are number of eggs per week.*

<table>
<thead>
<tr>
<th>Pivotal age in weeks</th>
<th>0.5</th>
<th>1.5</th>
<th>2.5</th>
<th>3.5</th>
<th>4.5</th>
<th>5.5</th>
<th>6.5</th>
<th>7.5</th>
<th>8.5</th>
<th>9.5</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 week</td>
<td>4</td>
<td>5</td>
<td>3</td>
<td>3</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>15</td>
</tr>
<tr>
<td>2 weeks</td>
<td>9</td>
<td>10</td>
<td>7</td>
<td>6</td>
<td>14</td>
<td>12</td>
<td>6</td>
<td>3</td>
<td>2</td>
<td>32</td>
<td></td>
</tr>
<tr>
<td>3 weeks</td>
<td>19</td>
<td>22</td>
<td>14</td>
<td>12</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>32</td>
<td>67</td>
<td></td>
</tr>
<tr>
<td>4 weeks</td>
<td>40</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>141</td>
</tr>
<tr>
<td>5 weeks</td>
<td>84</td>
<td>97</td>
<td>63</td>
<td>53</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>297</td>
<td></td>
</tr>
<tr>
<td>6 weeks</td>
<td>117</td>
<td>204</td>
<td>132</td>
<td>111</td>
<td>564</td>
<td>564</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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The intrinsic rate of natural increase of an insect population

season. Consideration of this is left to a later section of the discussion.

(2) For the calculation of the maximum intrinsic rate of increase the life table of the species from deposition of the egg (or larva) to the end of egg-laying life in the adult must be known. The starting-point of this life table is thus the stage which corresponds to the point of 'birth'. Deevey (1947) has noted that the point of universal biological equivalence for animals is doubtless fertilization of the ovum. But, from the point of view of the number of animals in the population and for purposes of calculating \( r \), a knowledge of pre-birth mortality is not required. For the calculation of \( r \) the life table beyond the end of reproductive life has no significance, but a knowledge of age-specific post-reproductive survival until the point of death is needed, on the other hand, for the calculation of the stable age distribution and the instantaneous birth-rate. This is evident from a consideration of the method of calculation shown in Table 4. The post-reproductive life assumes negligible significance in this particular example, but its importance in such calculations increases as \( r \) approaches a value of zero.

The relative importance of the survival pattern (i.e. the shape of the \( l_a \) curve) in determining the value of \( r \) is itself a function of \( r \). When \( r \) is small its value may be dependent to a significant extent on the oviposition in late adult life, when it is large it is mostly determined by the oviposition rates of adults in early adult life. When the intrinsic rate of increase is high and the life table of the adult follows the typical diagonal pattern (e.g. Pearl et al. 1941) with no high mortality in early adult life, consideration of the adult life table is of little importance in calculating \( r \). This is because survival rate is high in the ages which contribute most to the value of \( r \). In species which have a low intrinsic rate of increase the life table may assume more significance in determining the value of that rate of increase. More data are required before the importance of this point can be established. The pattern of survival which gives a maximum value of \( r \) has its maxima in the pre-reproductive and early reproductive stages. A knowledge of total survival of the immature stages is of course essential in all cases. More attention might well be given by entomologists to securing life table data than has been given in the past. Without it no true picture of the intrinsic rate of increase can be obtained.

(3) There remains to be considered the age distribution of the population in relation to its capacity to increase in numbers. In a population in an unlimited environment the stable age distribution is the only one which gives an unvarying value of \( r \). For this reason the stable age distribution is the only sound basis on which to make comparisons between different values for rates of increase (whether between different species or one species under different physical conditions). The actual age distribution of a population in nature may be quite different and its consideration is of importance in determining the initial advantage one form of distribution has over another. In an unlimited environment these initial differences in age composition are eventually ironed out. A population which initiates from a number of adults at the peak age of egg laying clearly has a higher initial rate of increase than one which starts from the same number in all different stages of development.

These considerations may be of most importance in temperate climates where there is a definite seasonal occurrence of active stages. The stage in which the insect overwinters or oversummers will determine the age distribution of the population which initiates the seasonal increase in the spring or in the autumn (whichever the case may be). The pea weevil, Bruchus pisorum, in California hibernates as an adult. With the first warm days in the spring the adults leave their overwintering quarters under bark and fly into the pea fields (Brindley, Chamberlin & Hinman, 1946). Following a meal of pollen they commence oviposition on the pea crops. This mode of initiating the spring population would be far more effective than one which started with the same number of insects in the egg stage. The overwintering adults begin their reproductive life at a much later age than the adults in the next generation. It would be of interest to know whether the age schedule of fecundity (taking the commencement of egg laying as zero age) is the same for both generations. This is a point which does not appear to have been investigated for insects which hibernate as adults. It is clearly of much importance in determining the intrinsic rate of increase of successive generations.

Overwintering as pupae must theoretically rank as the second most effective age distribution for initiating spring increase. Many species which overwinter as pupae would have a higher mortality if they overwintered as adults. The corn-ear worm, Heliothis armigera, for example, can hardly be conceived as overwintering as an adult moth in the North American corn belt. In the northern part of this belt even the pupae which are protected in the soil are unable to survive the winter. Recolonization evidently takes place each year from the warmer south (Hãsemann, 1931).

Overwintering in the egg stage (in hibernation or in diapause) is common in insects. Here again it is difficult to imagine the other stages of these orders as successfully hibernating. The grasshopper, Aotroicetes cruciata (Andrewartha, 1944), and the majority of aphids are examples of this. A minority of aphid species are, however, able to overwinter as apterae by finding protection in leaf axils and similar niches (Theobald, 1926), some others are enabled to
survive as adults by virtue of their symbiosis with ants (Cutright, 1925). The relatively vulnerable aphids find protection in the nests of ants. The ants not only carry them to their nests, but feed them during the winter months and with the return of spring plant them out on trees again!

Overwintering as nymphs or larvae is a rarer phenomenon except with species which can feed and grow at low temperatures and so are not hibernators. The active stages of the lucerne flea, *Smyrnthurus viridis*, for example, can be found in the winter in Australia (Davidson, 1934). The seasonal cycle of the reproducing population commences with the first rains in autumn; this population being initiated with oversummering eggs. The eggs are the only stage which are resistant to the dryness and high temperatures of the summer months. Species of insects with hardy adult stages like the weevil, *Otiarrhynchus cribripennis* (Andrewartha, 1933), aestivate as adults. An interesting case of a butterfly, *Melitaea phaeton*, aestivating as a quarter-grown larva at the base of its food plant is described by Hovanitz (1941).

The preceding examples illustrate how the age distributions of initiating populations vary in seasonal species. This depends on the nature of the overwintering or oversummering stage. The particular stage may have been selected in nature not only by virtue of its resistance to unfavourable physical conditions but also in relation to its merits in initiating rapid establishment of a population in the spring and autumn. The calculation of the initial and subsequent rates of increase of populations with these different types of age distribution is considerably more complicated than the calculation of intrinsic rates of increase for populations with stable age distributions. This problem is not dealt with in this paper and the reader is referred to Leslie (1945, p. 207 et seq.) for an outline of the principles involved in such calculations.

The length of the developmental stages, the age schedule of fecundity, the life table of the species and the age distribution of initiating populations present a pattern which has adaptive significance for the species. The analytic study of the intrinsic rate of increase of a species (as exemplified by *Calandra oryzae*) may throw light on the evolutionary significance of the life cycle of different species. Such a study must necessarily be related to the behaviour pattern of the insect and the type of environment it lives in. Nor can the importance of effects of density and competition be overlooked. These are, of course, studies in themselves beyond the scope of this paper.

8. SUMMARY

The parameter known as the intrinsic rate of natural increase, which was developed for demographic analyses by A. J. Lotka, is introduced as a useful concept for the study of insect populations. It is suggested that for the sake of uniformity of terminology in population biology and for precision of definition, that the term "intrinsic rate of natural increase" might be considered more appropriate than an alternative term "biotic-potential" which is more frequently used in relation to insect populations. The intrinsic rate of natural increase is defined as the exponent "r" in the exponential equation for population increase in an unlimited environment. The rate of increase of such a population is given by \( dN/dt = rN \). The parameter \( r \) refers to the rate of increase of a population with a certain fixed age distribution known as the stable age distribution. Both the intrinsic rate of natural increase and the stable age distribution may be calculated from the age-specific survival rates (life table) and age-specific fecundity rates. The methods of calculation are exemplified with data for the rice weevil, *Calandra oryzae* (L.), and some adapted from the flour beetle, *Tribolium confusum* Duval. It is shown in this example that the intrinsic rate of natural increase is determined to a much greater extent by the rate of oviposition in the first 2 weeks of adult life than by the total number of eggs laid in the entire life time. The oviposition rates in the first 2 weeks account for 85% of the value of \( r \) whereas only 27% of the total number of eggs are laid in that time. With each successive week in the life of the adult, eggs laid make a lessened contribution to the value of \( r \). The methods of calculation of \( r \) provide a means of determining the extent to which the various components—the life table, the fecundity table and the length of the pre-reproductive stages—enter into the value of \( r \). It is suggested that analyses of this sort may provide a clue to the life patterns characteristic of different species.

The importance of the age distribution of populations which initiate seasonal increase in the autumn and spring is discussed. These age distributions depend on the nature of the overwintering or oversummering stage. It is suggested that this particular stage, whether it be adult, larva, pupa or egg, has been selected by virtue not only of its resistance to the unfavourable season, but also in relation to its merits in initiating rapid establishment of a population in the succeeding season.

It is shown how the value of \( r \) for *Calandra oryzae* varies with temperature. Four other parameters are also defined: the net reproduction rate, the mean length of a generation, the infinitesimal birth-rate and the infinitesimal death-rate. The methods of calculation of these parameters are also exemplified with data for *C. oryzae*.

9. ACKNOWLEDGEMENTS

Grateful acknowledgement is made to the Director of the Bureau of Animal Population, Oxford University, Mr C. S. Elton, for the facilities of the Bureau.
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which were placed at the author's disposal during his term there as a visiting worker. Mr Elton provided much encouragement during the investigation. It is a pleasure to acknowledge too the inspiration and help of Mr P. H. Leslie of the Bureau of Animal Popula-
tion. His direction was indispensable in all mathem-
atical and actuarial aspects of the paper and his critical examination of the manuscript was much to its advantage.

REFERENCES

Andrewartha, H. G. (1933). 'The bionomics of
Otiornynchus crivicolli Gyll.' Bull. Ent. Res. 24:
373-84.

Andrewartha, H. G. (1944). 'The distribution of
plagues of Austrostictes cruciata Sauss. (Acrididae)
in relation to climate, vegetation and soil.' Trans. Roy.


Birch, L. C. (1945b). 'The influence of temperature on
the development of the different stages of Calandra
oryzae L. and Rhizopertha dominica Fab. (Coleoptera),'

Birch, L. C. (1945c). 'The influence of temperature, 
humidity and density on the oviposition of the small
strain of Calandra oryzae L. and Rhizopertha dominica

Birch, L. C. (1945d). 'The biotic potential of the small
strain of Calandra oryzae and Rhizopertha dominica.'

Birch, L. C. (1945e). 'The mortality of the immature
stages of Calandra oryzae L. (small strain) and Rhi-
zopertha dominica Fab. in wheat of different moisture

Birch, L. C. (1946). 'The heating of wheat stored in bulk

Brindley, T. A., Chamberlin, J. C. & Hinman, F. G.
(1940). 'The pea weevil and methods for its control.'

Chapman, R. N. (1931). 'Animal ecology with especial
reference to insects.' New York.

Crombie, A. C. (1945). 'On competition between
different species of graminivorous insects.' Proc. Roy.

Crombie, A. C. (1947). 'Interspecific competition.'

Cutright, C. R. (1925). 'Subterranean aphids of Ohio,'

Davidson, J. (1934). 'The "lucerne flea" Smytnthus
viridis L. (Collembola) in Australia.' Bull. Coun. Sci

trends in a natural population of Thrips imaginis Bagnall
(Thysanoptera).' (In the Press).

Deevey, E. S. (1947). 'Life tables for natural populations
of animals.' Biometrics, 3: 59-60.

Dublin, L. I. & Lotka, A. J. (1925). 'On the true rate of
natural increase as exemplified by the population of
the United States, 1920.' J. Amer. Statist. Ass. 20:
305-39.

New York.

Gause, G. F. (1934). 'The struggle for existence.'
Baltimore.

Hansen, L. (1925). 'Outbreak of corn earworm in
Missouri.' J. Econ. Ent. 24: 649-50.

Hovanitz, W. (1941). 'The selective value of aestivation
and hibernation in a Californian butterfly.' Bull.
Brooklyn Ent. Soc. 36: 133-6.

dioxide production as a measure of infestation of grain

population mathematics.' Biometrika, 33: 183-212.

Leslie, P. H. & Ranson, R. M. (1940). 'The mortality,
fertility and rate of natural increase of the vole (Microtus
agrestis) as observed in the laboratory.' J. Anim. Ecol.
9: 27-52.

Lotka, A. J. (1925). 'Elements of physical biology.'
Baltimore.

Lotka, A. J. (1927). 'The size of American families in the
eighteenth century and the significance of the empirical
constants in the Pearl-Reed law of population growth.'

Lotka, A. J. (1939). 'Théorie analytique des associations
biologiques. Deuxième Partie. Analyse démographique
avec application particulière à l'espèce humaine.'

Lotka, A. J. (1945). 'Population analysis as a chapter in the
mathematical theory of evolution.' In LeGros
Clark, W. E. & Medawar, P. B., 'Essays on Growth and

Maclagan, D. S. (1932). 'An ecological study of the
"lucerne flea" (Smytnthus viridis, Linn.)' Bull. Ent.
Res. 23: 101-90.

Pearl, R., Park, T. & Miner, J. R. (1941). 'Experimental
studies on the duration of life. XVI. Life tables for the
flour beetle Tribolium confusum Duval.' Amer. Nat.
75: 5-19.

Stanley, J. (1946). 'The environmental index, a new
parameter as applied to Tribolium.' Ecology, 27: 303-14.

Theobald, F. V. (1926). 'The plant lice of the Aphidinae

Thompson, W. R. (1931). 'On the reproduction of
organisms with overlapping generations.' Bull. Ent.
Res. 22: 147-72.

'Standard four-figure mathematical tables.' London.

Volterra, V. (1931). 'Leçons sur la théorie mathématique
de la lutte pour la vie.' Paris.